

SPATIAL AND TEMPORAL SHIFTS IN ESTUARINE NURSERY HABITATS
USED BY JUVENILE SOUTHERN FLOUNDER (*PARALICHTHYS LETHOSTIGMA*)

A Thesis

by

NATHANIEL B. FUREY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Wildlife and Fisheries Sciences

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Flounder (*Paralichthys lethostigma*)
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Approved by:

Chair of Committee,	Jay R. Rooker
Committee Members,	Kirk O. Winemiller
	Timothy Dellapenna
Head of Department,	John Carey

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ABSTRACT

Spatial and Temporal Shifts in Estuarine Nursery Habitats Used by Juvenile Southern
Flounder (*Paralichthys lethostigma*). (August 2012)

Nathaniel B. Furey, B.S., University of New England

Chair of Advisory Committee: Dr. Jay R. Rooker

Southern flounder (*Paralichthys lethostigma*) is a recreationally and commercially important flatfish species found in the Gulf of Mexico, and recent analyses indicate that the northern Gulf of Mexico population is in decline. For proper management, knowledge of habitats used throughout the juvenile stage is needed. The aim of the current study is to examine habitat use of young-of-year (YOY) southern flounder in the Galveston Bay complex using habitat distribution models and acoustic telemetry. A set of habitat distribution models examined how habitat use changes during the first year of life. In addition, southern flounder were tagged with acoustic telemetry transmitters and monitored with a novel receiver array that allows for measurements of fine-scale movements. These movements were compared to habitat maps to examine habitat selection. Habitat distribution models determined that habitat requirements for southern flounder change with ontogeny and season. Newly settled southern flounder were most influenced by physicochemical parameters and the presence of seagrass beds. YOY southern flounder, however, showed increased occurrence at freshwater inlets during summer and fall months, and occurrence decreased at tidal inlets during the fall.

Predictions of habitat suitability across the Galveston Bay complex indicate that the factors influencing occurrence of southern flounder change with season, ontogeny, and availability of suitable habitats. With acoustic telemetry, it was apparent that habitat use by southern flounder was nonrandom and influenced by benthic and other physicochemical conditions. Habitat analyses indicated that southern flounder used sand habitats more frequently than seagrass, oyster reef, or salt marsh habitats. Telemetry results also indicated that depth and water temperature were important determinants of habitat suitability for YOY southern flounder, with individuals preferring deeper and cooler regions of the water column in Christmas Bay. Both model and telemetry analyses indicate that habitat use by YOY southern flounder is dynamic across multiple spatial and temporal scales, with distributions and movements influenced strongly by ontogenetic changes in habitat associations, temporal and spatial variability in physicochemical conditions, and tidal cycles.

DEDICATION

This thesis is dedicated to my sisters Allison and Rachel Furey, my parents Bruce and Nancy Redman-Furey, and my girlfriend Laura Hilbert for their never-wavering support and confidence in my ability.

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TABLE OF CONTENTS

	Page
ABSTRACT	iii
DEDICATION	v
ACKNOWLEDGEMENTS	vi
TABLE OF CONTENTS	vii
LIST OF FIGURES.....	viii
LIST OF TABLES	ix
CHAPTER	
I INTRODUCTION.....	1
II ASSESSING HABITAT SUITABILITY FOR JUVENILE SOUTHERN FLOUNDER (<i>PARALICHTHYS LETOSTIGMA</i>)	4
Introduction	4
Methods	6
Results	15
Discussion	22
III FINE-SCALE MOVEMENTS AND HABITAT USE OF JUVENILE SOUTHERN FLOUNDER (<i>PARALICHTHYS LETHOSTIGMA</i>) IN AN ESTUARINE SEASCAPE.....	30
Introduction	30
Methods	32
Results	41
Discussion	48
IV SUMMARY AND CONCLUSIONS.....	53
REFERENCES	55
VITA	66

LIST OF FIGURES

	Page
Figure 1 Galveston Bay Complex (GBC) location within the Gulf of Mexico	15
Figure 2 Response curves of the relationships among explanatory variables and juvenile southern flounder occurrence for each life stage as generated through generalized additive models	16
Figure 3 Spatial distribution of predicted habitat suitability for juvenile southern flounder across the Galveston Bay Complex in February, June, and September of 2005, corresponding to models generated for the newly settled, YOY-summer, and YOY-fall life stages, respectively.....	20
Figure 4 The proportion of each region (as depicted in Figure 1) that contains highly suitable habitat (top 10% of predicted values per life stage).....	21
Figure 5 The location of the study area in Christmas Bay, Texas	33
Figure 6 YOY southern flounder with acoustic tag externally attached	35
Figure 7 Detections of YOY southern flounder within the VPS array	43
Figure 8 Mean EDA ratios of habitat types available to southern flounder within the study area	46
Figure 9 Response plots of explanatory covariates on the occurrence of southern flounder tracked with acoustic telemetry as analyzed with GAM	47

LIST OF TABLES

	Page
Table 1 Summary of data used and mean and standard deviation (SD) of explanatory variables evaluated with GAMs to examine habitat-species relationships for juvenile southern flounder.	10
Table 2 Comparison of fit among models for each season or life stage based on model flexibility (Max df)	13
Table 3 Summary of recorded detections for tagged southern flounder.	36
Table 4 Summary of habitat composition within the VPS array	45

CHAPTER I

INTRODUCTION

Southern flounder (*Parlichthys lethostigma*) is a recreationally and commercially important flatfish species of the family Paralichthyidae. Southern flounder are found throughout both the south Atlantic and Gulf of Mexico coasts in bays, estuaries, and coastal waters. Adult southern flounder generally inhabit bays and estuaries throughout the year, and spawning occurs at tidal passes and coastal waters in late winter (November through January). Eggs and larvae are dependent upon physical transport into the estuaries prior to hatching, which occurs from December through early February (Glass et al. 2008). Settlement in nursery habitats occurs at lengths less than 10 mm, and growth rates through the settlement stage are approximately 0.4 mm/d (Glass et al. 2008). Southern flounder generally reach sizes between 200 and 330 mm total length (TL) by the end of the first year (Fischer and Thompson 2004), with a mean size of approximately 250 mm TL in Texas waters (Stunz et al. 2000). Female southern flounder become sexually mature at age 2 or 3 with half of the population becoming mature at 385 mm TL (Smith and Scharf 2010). The southern flounder fishery has been popular historically, with approximately 250,000 fish landed annually in Texas during the 1980's (Weixelman et al. 1992).

Recent surveys and a time series analysis indicate that southern flounder population in Texas is in decline (Froeschke et al. 2011). In response,

This thesis follows the style of Journal of Sea Research.

2009 bag limits were reduced by one half (five fish daily for recreational anglers and fifteen daily for commercial guides), and a stock enhancement program was initiated. For proper management to occur, fishery scientists need to know habitats required by southern flounder during the critical first year of life (Beck et al. 2001). It is also important to recognize that habitat requirements can change dramatically with ontogeny, especially for fishes with an estuarine residency period (Grober-Dunsmore et al. 2009). Therefore, definitions of required habitats need to be specific to ontogenetic stage, even during the first year of life.

There are a number of methods for analyzing habitat use of estuarine fishes. When large datasets are available, habitat distribution models can efficiently relate the distribution of marine organisms to environmental conditions (Valavanis et al. 2008). Multiple forms of habitat distribution models exist, including boosted regression trees, maximum entropy approaches, and generalized additive models (GAM). GAMs are a nonparametric extension of generalized linear models, and allow for a flexible relationship between the response and explanatory variables (Wood 2006). Investigations of habitat use can be conducted with conventional tags, natural tracers, or acoustic telemetry. Of these approaches, acoustic telemetry is the best method to record fine-scale movements, and the recent development of positioning systems now allows for in-situ measurements of habitat use with a resolution of less than 5 m (Espinoza et al. 2011b).

The purpose of this study was to examine habitat use by young-of-year (YOY) southern flounder within the Galveston Bay complex using both habitat distribution

models and acoustic telemetry. A set of GAMs examined how habitat use may change with ontogeny and/or season throughout the first year of life with the use of a long-term dataset collected by the Texas Parks and Wildlife Department (TWPD) (Chapter II). In addition, southern flounder were tagged with acoustic telemetry transmitters and monitored with a novel passive acoustic receiver array that allows for measurements of fine-scale movements. These movements were compared to habitat maps to examine habitat selection (Chapter III). Working hypotheses are 1) that southern flounder habitat use, as examined with GAMs, will change with ontogeny or season due to expected changes in physicochemical tolerances and behavior, and 2) that habitat use will be nonrandom, as measured with acoustic telemetry because of the potential ecological benefits of certain habitat types.

CHAPTER II

ASSESSING HABITAT SUITABILITY FOR JUVENILE SOUTHERN FLOUNDER
(*PARALICHTHYS LETOSTIGMA*)

Introduction

Estuarine habitats support high densities of many fish and invertebrate species, and are often considered nurseries (Beck et al. 2001, Boesch and Turner 1984). Within estuaries, site-specific differences in benthic and physicochemical characteristics lead to variability in habitat quality, and subsequent distributions of juveniles (Beck et al. 2001). Identifying factors that influence the distribution and abundance of organisms across estuarine seascapes is needed to define nursery habitats of commercially or recreationally important species. Most studies investigating factors affecting distributions among potential nursery habitats focus on newly settled individuals immediately after estuarine ingress when mortality is at its highest (Almany and Webster 2006, Levin 1991, Victor 1986). Mortality rates of teleost fishes often remain elevated throughout the juvenile period (Able et al. 2007) and vary as a function of the estuarine habitats used (Minello et al. 2003, Rooker et al. 1998). Furthermore, habitat requirements can change during ontogeny, even within the same estuarine seascape (Grober-Dunsmore et al. 2009). In response, life-stage-specific habitat requirements are needed for the entire period of estuarine residency and, to date, few studies have attempted to simultaneously compare distributions of multiple size/age groups during the juvenile period (but see Stoner et al. 2001).

Habitat distribution models have become a common method to identify factors influencing species occurrence and subsequently to visualize the spatial arrangement of habitats in estuarine and marine systems (Valavanis et al. 2008). Currently, a number of methods exist for generating habitat distribution models, including classification regression trees, maximum entropy approaches, general linear models, and generalized additive models. Generalized additive models (GAMs) are extensions of general linear models that allow the inclusion of both parametric and nonparametric effects of explanatory variables on the response (Wood and Augustin 2002, Wood 2006), and GAMs have been used to successfully identify factors influencing habitat requirements of a wide variety of estuarine-dependent fishes, including spotted seatrout (*Cynoscion nebulosus*) (Kupschus 2003), winter flounder (*Paralichthys pseudoamericanus*) (Stoner et al. 2001), and juvenile Pacific cod (*Gadus macrocephalus*) (Abookire et al. 2007). More recently, GAMs have been used to identify factors influencing suitable estuarine habitats of juvenile flatfish, allowing for the generation of nursery habitat maps in order to guide habitat conservation and fisheries management (Florin et al. 2009, Zuchetta et al. 2010).

The purpose of this study was to develop habitat distribution models for characterizing the spatial occurrence of suitable habitat of juvenile southern flounder (*Paralichthys lethostigma*) across a large estuarine complex. Southern flounder is a recreationally important flatfish found in coastal waters throughout the Gulf of Mexico, and due to recent declines in population numbers (Froeschke et al. 2011), there is a renewed interest in defining essential habitats of this species, particularly during the first

year of life when mortality is high and variable for fishes (Houde 1989, Winemiller and Rose 1992, Winemiller 2005). It has been suggested that the coupling of biotic and abiotic factors drive the distribution of juvenile southern flounder within estuarine habitats (Burke 1995, Fitzhugh et al. 1996). More specifically, benthic types and physicochemical conditions of the water column appear to influence the distribution and possibly growth and survival of southern flounder (Burke et al. 1991, Del Toro-Silva et al. 2008, Minello et al. 1987). Here, a GAM framework was used to examine the relative importance of temporal, physicochemical, and benthic factors on the distribution of newly settled and young-of-the-year southern flounder. By partitioning the first year of life into discrete life history intervals, ontogenetic and seasonal changes in species-habitat relationships of southern flounder are comprehensively examined.

Methods

Data Used in Modeling

Data used in models were based on monthly fishery-independent surveys of the Galveston Bay Complex (GBC) by the Texas Parks and Wildlife Department (TPWD) from 1999-2009. Surveys were conducted using bag seines (18.3 m long, 1.8 m deep, 13 mm mesh in the cod end). Bag seines were pulled in shallow water habitats (2 m maximum depth) parallel to shore for a distance of approximately 15 m (Martinez-Andrade et. al 2005). Juvenile southern flounder captured in surveys were enumerated and measured for total length (TL). TPWD recorded location and numerous environmental variables, including water temperature, salinity, dissolved oxygen,

sediment types present, and depth. Sediment types recorded by TPWD were simplified to presence of sand, mud, and rocks to reduce the number of explanatory variables used in modeling. In addition, catch data for juvenile southern flounder were separated into three life stages based on size and month of the year. First, the ‘newly settled’ life stage is defined as individuals captured in the months December through March less than 50 mm total length (TL), which is conservative given growth rates (up to 0.76 mm/day) and hatch dates (predominantly mid December to January) observed by Glass et al. (2008) in Galveston Bay. ‘YOY’ southern flounder were defined as individuals 50 mm to 200 mm TL and this represents the remainder of the age-0 period well after the winter settlement event. Two YOY life stages were defined using the seasonal periods of April to July and August to November, to further examine ontogenetic and/or seasonal shifts in distribution or habitat use, which for simplicity will be referred to as summer and fall, respectively. Given that the mean size of age-0 southern flounder observed by Stunz et al. (2000) along the Texas coast was 254 mm TL, I am confident that all individuals in the YOY category were less than one year of age. All survey locations were visualized and all spatial analyses were conducted in ArcGIS 9.3 (ESRI, Redlands CA).

Within a Geographic Information System (GIS), variables of distance to benthic habitats (marsh edge, seagrass, oyster reef) and sources of fresh and marine water (freshwater inlets and tidal inlets) were created for each bag seine sample. Marsh edges were defined from georeferenced National Wetlands Inventory maps (NWI; Cowardin et al. 1979). Marsh habitats were defined as Estuarine Intertidal Emergent Persistent vegetation within the NWI habitat classification scheme (E2EM1; Cowardin et al. 1979).

Oyster reef and seagrass locations were downloaded from the National Oceanographic Atmospheric Administration National Coastal Data Development Center (NOAA NCDDC) and were originally defined by the Texas General Land Office (GLO). Distances were calculated between features with the shoreline as a barrier using the cost-distance function within ArcGIS (ESRI, Redlands CA). In addition, monthly surface freshwater inflow values were generated by Texas Water Development Board (TWDB) hydrography models for Galveston Bay (available at http://midgewater.twdb.state.tx.us/bays_estuaries/hydrologypage.html).

Because unstable habitats may prevent fish from ever experiencing optimal conditions (Peterson 2003), the variance of a location's physicochemical conditions was estimated and included in the modeling process. Temperature variance was defined as the variance in recorded temperatures from all surveys within the same season (newly settled season, summer, or fall) and within 1 minute (1/60 degree) of latitude and longitude. Variance in dissolved oxygen and salinity were collinear and, as a result, a metric was generated by the summation of variances in the two conditions using the same temporal and spatial scales as temperature variance.

Model Generation

To examine the factors affecting southern flounder occurrence, generalized additive models (GAMs) were employed (Hastie and Tibshirani 1990, Wood 2006). GAMs are a nonparametric extension of general linear models (GLM), and provide the

flexibility to model non-parametric relationships that can be seen in ecology. In the case of binomial GAMs with a logit link, the equation takes the form of

$$\ln \left[\frac{1 - y^*}{y^*} \right] = \beta_0 + \sum_k f_k x_k$$

Where y^* represents the predicted probability of southern flounder occurrence, β_0 equals the intercept, k equals the number of explanatory variables included in the model, f_k equals the smoothing function for the variable x_k . Penalized cubic regression splines determined the shape of nonparametric functions, with the degree of smoothing selected automatically for models and were generated within the “mgcv” library (Wood 2006, Wood 2008) using R 2.10 software (R Development Core Team 2010).

Three different life stages of juvenile southern flounder were modeled: 1) newly settled, 2) YOY-summer, and 3) YOY-fall. The season and life stage definitions used resulted in a total of 2500 surveys from 2455 unique sites, with 196 surveys observing appropriately sized southern flounder (Table 1). Manual backward stepwise selection based on minimization of the Akaike information criterion (AIC; Akaike 1974) was used to select final models. Prior to model selection, collinearity was explored among abiotic variables using Spearman correlation coefficient (Spearman ρ). When the Spearman ρ between two variables > 0.5 , the effect of each variable on southern flounder occurrence was examined alone within a separate GAM. The variable that indicated better model fit was entered in the initial model prior to backwards selection, while the other variable was discarded (Guisan and Thuiller 2005).

To prevent overfitting, the gamma parameter was set to 1.4 in all models, as suggested in Wood (2006), and each explanatory variable was given a maximum of number of degrees of freedom (df) as suggested in Ciannelli et al. (2008).

Table 1: Summary of data used and mean and standard deviation (SD) of explanatory variables evaluated with GAMs to examine habitat-species relationships for juvenile southern flounder. *Prevalence is based on *a priori* size limits for each life stage as described in the Methods (Chapter II).

	Newly Settled		YOY – Summer		YOY - Fall	
number of surveys	865		872		863	
flounder prevalence*	0.09		0.08		0.03	
	Mean	SD	Mean	SD	Mean	SD
Temperature (°C)	16.3	4.1	27.9	3.7	26.3	5.2
Salinity (PSU)	16.0	8.8	16.6	9.1	17.9	9.5
Depth (m)	0.4	0.2	0.6	0.3	0.6	0.3
Turbidity (NTU)	39.9	57.6	41.2	55.9	30.2	35.1
dissolved oxygen (ppm)	7.9	1.8	6.1	1.4	6.2	1.7
distance to fresh water (m)	15,193	10,096	14,931	9,830	14,472	9,740
distance to seagrass (m)	13,381	11,724	13,459	11,527	13,155	11,475
distance to tidal inlet (m)	17,874	14,308	17,371	13,706	17,996	13,960
distance to marsh (m)	635	1,174	629	1102	680	1,176
distance to oyster reef (m)	3,097	3,773	2,842	3,506	3,015	3,700
Flow	1,112,625	876,151	1,164,364	965,230	1,021,328	790,498
% mud	76.3		77.3		76.5	
% sand	76.1		77.2		76.6	
% rock	3.9		5.1		3.7	

As the number of df increases for each predictor, flexibility increases, as well as the probability of overfitting. The maximum number df is decided *a priori*, but the actual limit used varies among studies. Many studies employ a limit of 4 df per explanatory variable (Lehmann et al. 2002, Weber and McClatchie 2010, Zuchetta et al. 2010, and

others), but Sandman et al. (2008) suggest a maximum number of degrees of freedom of 2 or 3. Sandman et al. (2008) demonstrated that within model fit generally increases with increasing GAM flexibility, but fit to validation data often decreases simultaneously (indicating a lack of transferability or predictive capabilities). To examine the effects of varying model complexity, three initial models of increasing complexity (2, 3, or 4 df for each continuous explanatory variable) were examined with backward selection for each life stage of interest. After these three models were reduced via backward selection, a final model for each life stage was selected based on model fit to validation data (as described later in Model Calibration/Validation). Within-model performance was evaluated by percent deviance explained, AIC, and Area Under the Receiver Operating Characteristic Curve (AUC). AUC values are threshold-independent and range from 0 and 1, and depict a model's ability to determine occurrence or absence at a given site. A value of 0.5 indicates no predictive capability and a value of 1 indicates perfect predictive capability. Within model AUC values were calculated using the ROCR package in R (Sing et al. 2009).

Model Calibration/Validation

To evaluate the predictive abilities of GAMs, TPWD data from 1999-2009 were randomly split into training and validation datasets, with each dataset having equal number of surveys. Variable selection for GAMs was conducted using the training data, and the response functions of retained explanatory variables for each life stage were then

used to predict responses within the evaluation dataset. Model fits to validation datasets were evaluated by calculating AUC, sensitivity (the proportion of occurrences correctly predicted), and specificity (the proportion of absences correctly predicted) based on the threshold p_{fair} , at which the difference between sensitivity and specificity is minimized (Jensen et al. 2005, Jiménez-Valverde and Lobo 2007). AUC, sensitivity, and specificity, along with corresponding thresholds, were calculated in the “PresenceAbsence” library (Freeman 2007). From the three models (with 2, 3, or 4 maximum df per explanatory variable) for each life stage, sensitivity, specificity, and validation-AUC were compared to choose an optimal model for visualizing the spatial distribution of suitable habitats. Similar to Sandman et al. (2008), models with a maximum of 2 or 3 df resulted in the best fit for validation data (Table 2), with the final newly settled and YOY-fall models utilizing a maximum of 2 df and the final YOY-summer model utilizing a maximum of 3 df.

Table 2: Comparison of fit among models for each season or life stage based on model flexibility (Max df). Values in bold indicate the model with best fit to validation data, and thus selected as the final model for the respective life stage/season for use in habitat visualization. Sensitivity and specificity values were calculated based on an optimized threshold, ρ_{fair} , as described in the Methods.

Life stage	Newly settled			Young-of-the-year					
Season				Summer			Fall		
Within Model Measures of Fit									
Df	2	3	4	2	3	4	2	3	4
% Dev Explained	40%	42.3%	53.9%	23.4%	27.0%	33.1%	28.6%	42.7%	33.9%
Within Model AUC	0.92	0.93	0.96	0.81	0.84	0.87	0.92	0.96	0.92
Validation Measures of Fit									
Validation AUC	0.81	0.8	0.78	0.65	0.68	0.67	0.71	0.65	0.62
ρ_{fair}	0.05	0.05	0.05	0.06	0.07	0.07	0.01	0.01	0.01
Sensitivity	0.76	0.68	0.73	0.67	0.63	0.63	0.69	0.54	0.54
Specificity	0.72	0.71	0.66	0.57	0.64	0.62	0.65	0.71	0.67

Habitat Mapping and Visualization

After optimal models were selected for each life stage, GAMs were used to predict the probability of southern flounder occurrence across the GBC to visualize habitat suitability. Surfaces of 500 m² resolution were generated for all areas of the GBC less than or equal to 2 m in depth using bathymetry data from NOAA hydrographic sounding surveys (Taylor et al. 2008). For all locations, distances to benthic habitats and sources of fresh and marine water were calculated. Dissolved oxygen and turbidity were interpolated throughout the GBC using inverse distance weighting from TPWD survey data for each season in 2005. Temperatures were calculated by averaging images derived

from blended multiproduct sea surface temperature (SST) data downloaded from the NOAA CoastWatch Live Access Server (Feldman et al. 2011, Ocean Watch 2011). Gaps in SST data were removed via interpolation within the Spatial Analyst Toolbox in ArcGIS (ESRI, Redlands CA). Salinity values were based on monthly bay-wide contours generated by TWDB TxBLEND hydrography models (Longley 1994, Powell et al. 2002). After all explanatory variables were linked to the prediction grids, the “predict.gam” function in the “mgcv” library (Wood 2006, Wood 2008) was used to predict the probability of southern flounder occurrence given the seasonal conditions of 2005. Once each grid point contained a predicted value, suitable habitats were visualized as raster surfaces with a pixel size of 500 m². The highest 10% of predicted values were labeled as being within of one of three geographic regions of the GBC: Upper Bay, Lower Bay, or West Bay (Figure 1). The proportion of each region’s shallow habitats (less than 2-m depth) that was considered highly suitable in 2005 was calculated.

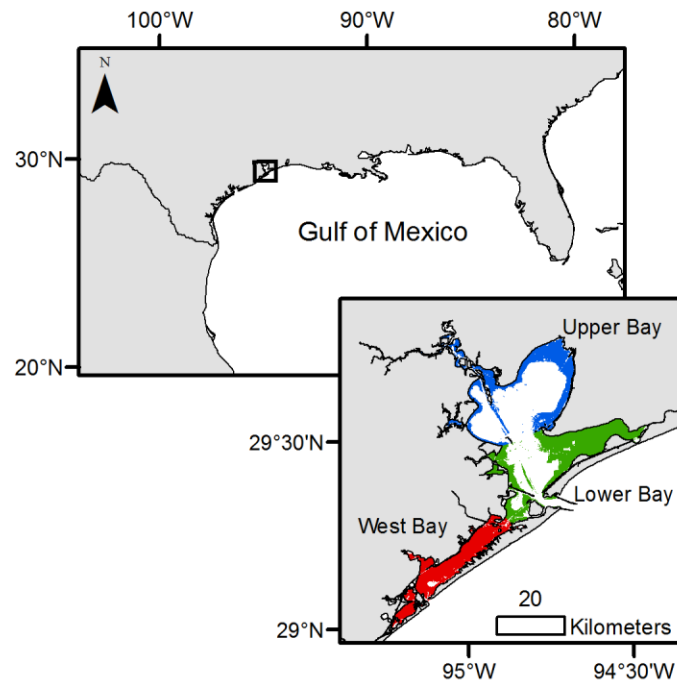


Figure 1: Galveston Bay Complex (GBC) location within the Gulf of Mexico. Shaded portions denote waters less than 2 m depth, and are separated into three regions for analysis of the spatial distribution of suitable habitats.

Results

The number of explanatory variables retained within the three final models ranged between five and seven (Figure 2). Relationships between the presence of mud, presence of sand, and monthly freshwater inflow with both temporal variables (year and month) were found to be collinear (Spearman $\rho > 0.5$). Therefore, only one variable from each pair was allowed to enter the initial models prior to stepwise selection.

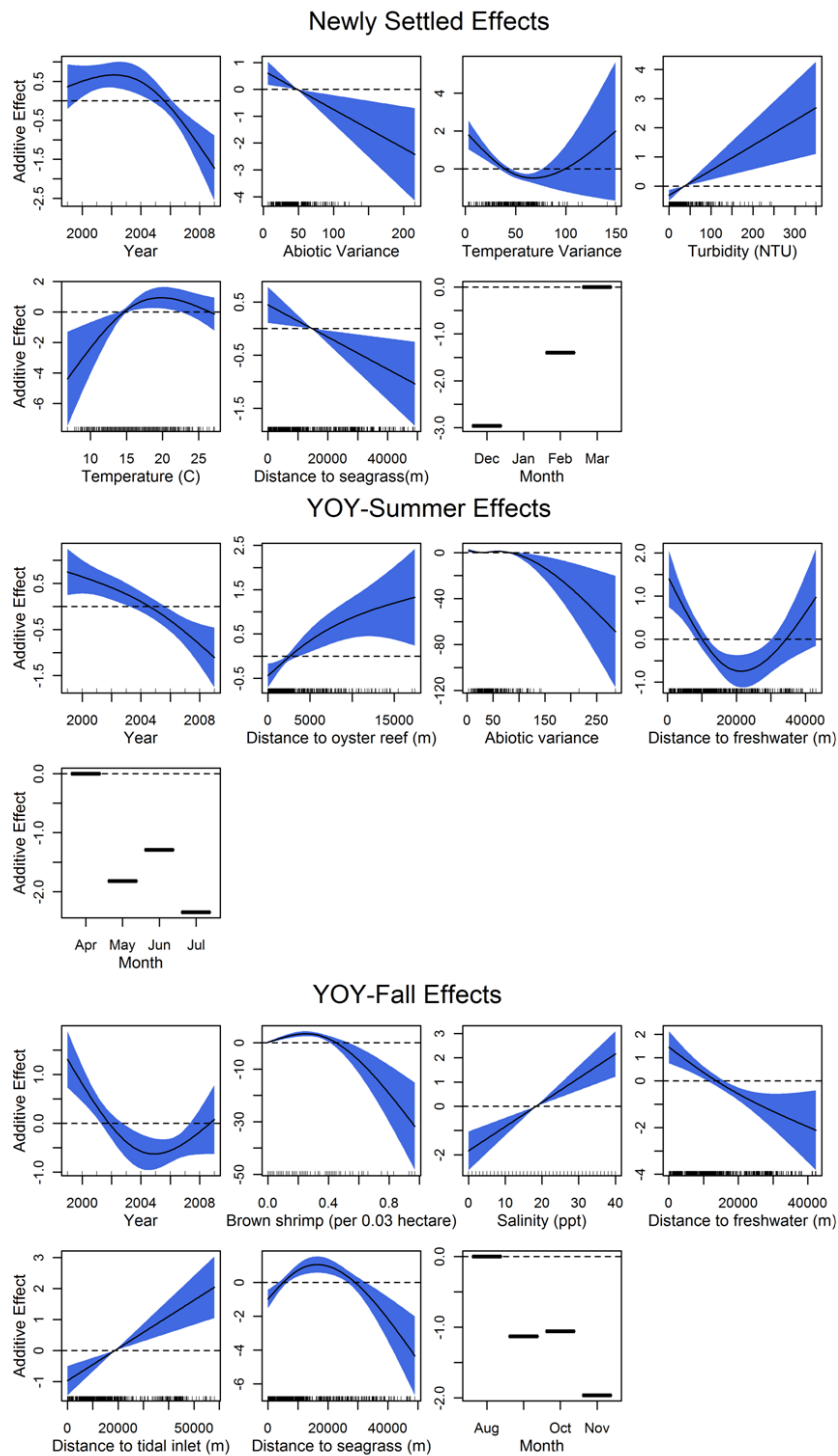


Figure 2: Response curves of the relationships among explanatory variables and juvenile southern flounder occurrence for each life stage as generated through generalized additive models.

Only two variables (month and year) were retained in all three final models, while six variables (depth, DO, presence of mud, presence of sand, monthly flow, and distance to marsh) were never retained in any of the final models. Each final model retained at least one variable unique from the other models.

Temporal Effects

Inter-annual variability in the occurrence of southern flounder was detected and the year variable was retained in all models. In general, occurrence of all life stages of southern flounder declined throughout the study period. Month was also retained in all final models, suggesting that occurrence also varied as a function of season (intra-annual effect). The newly settled model indicated a progressive increase in southern flounder occurrence throughout the season, with occurrence being lowest in December. For the YOY-summer and YOY-fall models, southern flounder occurrence declined throughout each life stage.

Benthic Effects

Among benthic effects, only distance to seagrass was retained in the newly settled model, and southern flounder occurrence increased at sites near seagrass. In the YOY-summer model, the variable distance to oyster reefs was retained, with areas less than 2 km from oyster reefs having low southern flounder occurrence. Within the YOY-fall model, distance to seagrass was retained, with occurrence peaking at intermediate distances (between approximately 5 and 25 km). In addition, brown shrimp abundance

was retained in the YOY-fall model. Southern flounder occurrence increased at sites with intermediate abundances of brown shrimp.

Physicochemical Effects

For the newly settled life stage, both temperature and turbidity maintained positive relationships with southern flounder occurrence. Temperatures greater than 16° C and turbidities of greater than 40 NTU resulted in a higher probability of southern flounder occurrence. Within the YOY-fall model, salinity was retained, and southern flounder occurrence increased in regions of the GBC with higher salinities (above 20 ppt).

Both measures of physicochemical variance (temperature variance and abiotic variance) maintained a negative association with southern flounder occurrence in the newly settled model. Abiotic variance was also retained in the YOY-summer model, with lower southern flounder occurrence when variance was high.

Distance to freshwater sources was retained in the YOY-summer model, with southern flounder occurrence highest at locations close to (<1 km) or farther (>3.5 km) from a freshwater source in the summer. The YOY-fall model also indicated that southern flounder occurrence was higher near freshwater sources, with occurrence declining at distances greater than 20 km from the freshwater source. An association with sources of marine water (tidal inlets) also was observed in the YOY-fall model, and distances greater than 20 km from tidal inlets resulted in higher occurrence.

Spatial Distribution of Habitat Suitability

The spatial distribution of predicted suitable habitat for 2005 across the GBC varied seasonally (Figure 3). The newly settled model predicted both a single large ($>20 \text{ km}^2$) patch and multiple smaller patches ($1\text{-}9 \text{ km}^2$) of highly suitable habitat within West Bay, and 29% of this bay contained highly suitable habitat (Figure 3, Figure 4). For the YOY-summer model, a large patch (51 km^2) of highly suitable habitat was predicted near the Trinity River inlet along with a number of small patches ($<5 \text{ km}^2$) of highly suitable habitats near the San Jacinto River inlet within the Upper Bay. A large area of contiguous patches (43 km^2) of highly suitable habitats by the San Jacinto River inlet was also predicted by the YOY-fall model in addition to a patch of highly suitable habitat 18 km^2 in West Bay. Thirty percent of West Bay contained highly suitable habitat for the YOY-summer life stage of 2005, while highly suitable habitat was found in 19% of West Bay for the YOY-fall life stage. Predicted suitability was relatively low in the Lower Bay during all three seasons, with only 4% of this bay containing highly suitable habitat in February 2005, and both YOY life stages containing even less (Figure 3, Figure 4).

Final Model Fit and Validation

Within-model fit, measured by AUC, was greater than 0.83 for all models (Table 2). Final models for southern flounder maximized validation AUC values, and the three models explained between 27.0% and 40.0% of residual deviance. Model fit to

validation data were slightly lower, with a validation AUC values of 0.81, 0.68, and 0.71 for the newly settled, YOY-fall, and YOY-summer models, respectively.

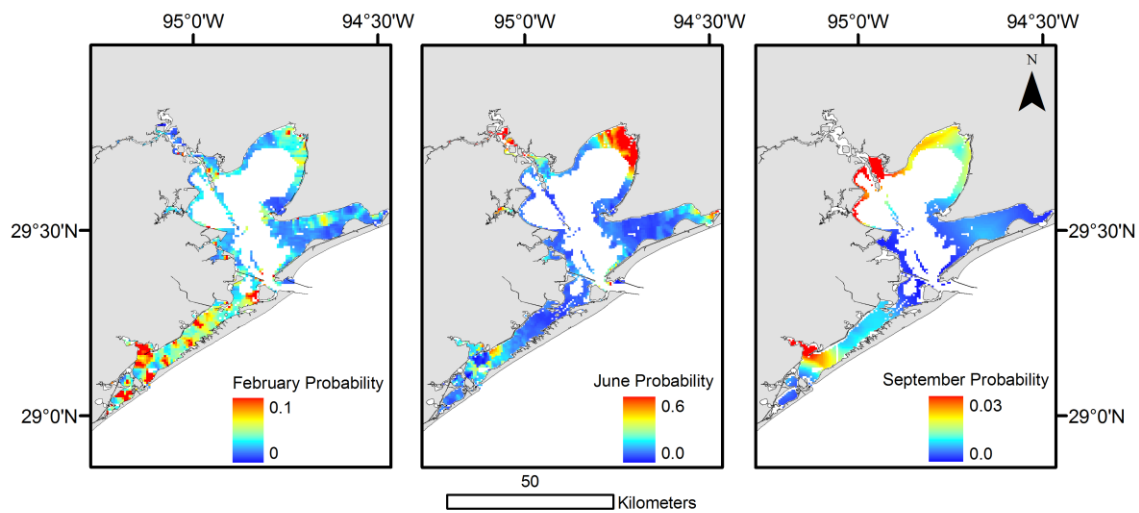


Figure 3: Spatial distribution of predicted habitat suitability for juvenile southern flounder across the Galveston Bay Complex in February, June, and September of 2005, corresponding to models generated for the newly settled, YOY-summer, and YOY-fall life stages, respectively.

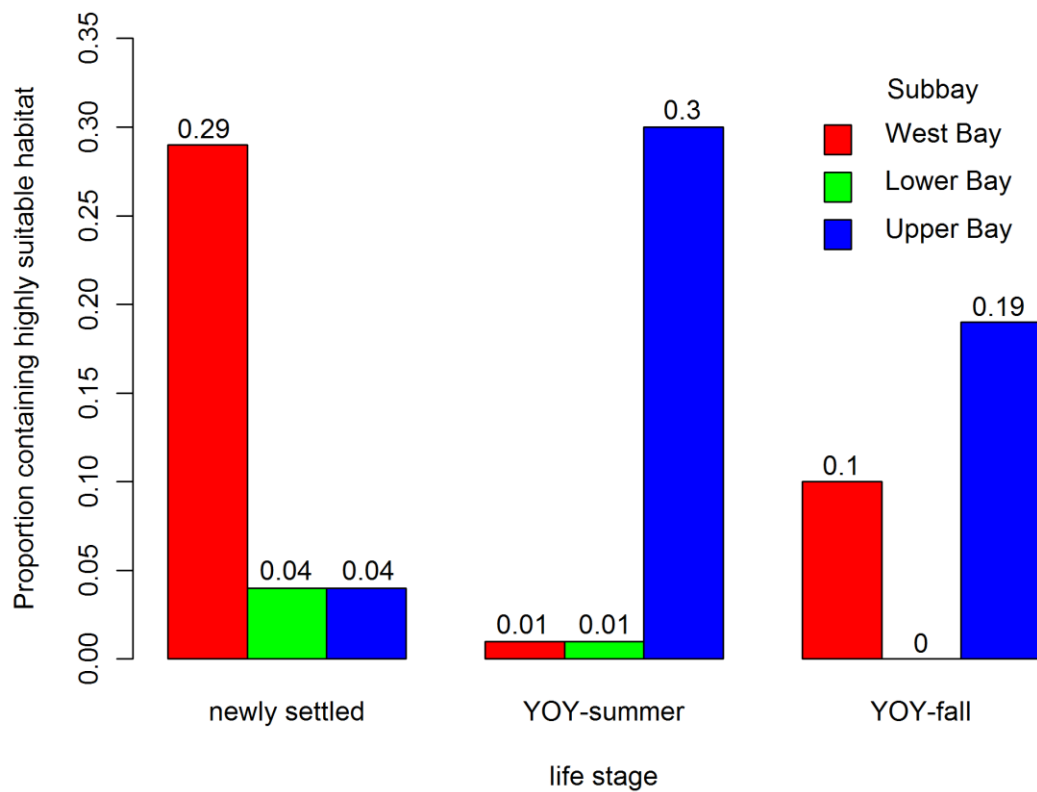


Figure 4: The proportion of each region (as depicted in Figure 1) that contains highly suitable habitat (top 10% of predicted values per life stage).

Sensitivity (percent of occurrences correctly predicted) ranged between 0.63 and 0.76, and specificity (percent of absences correctly predicted) ranged between 0.64 and 0.72. All measures of fit to validation data (validation AUC, sensitivity, and specificity) were highest for the newly settled model, and lowest for the YOY-summer model.

Discussion

The occurrence of juvenile southern flounder in the large estuarine seascape of the GBC varied both within and across years and both temporal variables (year and month) were retained in all three final models. Response curves indicated a relative decline in southern flounder occurrence within the GBC for all life stages, which is in accord with other studies reporting declines in the abundance of juvenile southern flounder in Texas (Froeschke et al. 2011, Nanez-James et al. 2009). Newly settled southern flounder increased in occurrence throughout the season, corresponding to the timing of larval influx into the estuary and subsequent winter settlement, and it appears that southern flounder are fully recruited to the estuary by the end of March. Both the YOY-summer and YOY-fall models are characterized by a general decline in southern flounder occurrence over time, which is expected due to natural mortality experienced by each cohort. Reduced catchability of larger southern flounder by bag seine may also contribute to the observed decline in southern flounder through both YOY life stages. Both intra- and inter-annual variations in occurrence suggest that other factors may influence the distribution and abundance of southern flounder population within the GBC. Taylor et al. (2010) found that winter winds and freshwater discharge heavily influenced recruitment variability of southern flounder in North Carolina estuaries. Although not examined in the current study, physical processes also could influence the transport of southern flounder prior to settlement, thus influencing their distribution in the GBC. Studies modeling transport have demonstrated strong correlations between larval fish pulses into Texas bay systems and physical processes occurring along the

Texas coast, further indicating the influence of physical transport on recruitment success (Brown et al. 2004, Brown et al. 2005).

Estuarine habitats can enhance the growth and/or survival of juvenile fishes, resulting in higher abundances of newly settled and YOY individuals within these habitats (Minello et al. 2003). The distance to specific habitat types was shown to affect southern flounder occurrence within the GBC. Distance to seagrass was retained in the model for newly settled southern flounder, and occurrence was higher near seagrass beds. Seagrass beds have been shown to support high densities of juveniles within estuaries (Heck et al. 2003) because these habitats provide shelter from predators and are often associated with greater prey biomass (Beck et al. 2001). It appears that seagrass beds within the GBC are important habitats for newly settled southern flounder when compared to other potential nursery habitats (marsh edge or oyster reef), as suggested by Nanez-James et al. (2009). Distance to seagrass was also retained in the YOY-fall model; however, it appears that this habitat's importance decreases with ontogeny, even within the first year of life. Other nursery habitat types investigated included salt marshes and oyster reefs. Distance to salt marsh edge was never retained, and although salt marshes have been identified as important nursery habitat for crustaceans and fishes (Minello et al. 2003), they did not appear to influence the distribution of juvenile southern flounder within the GBC over the years investigated. Oyster reefs were only retained in one model (YOY-summer), and the finding of reduced occurrence near oyster reefs agrees with other studies, which may be due to reductions in prey or increases in predation pressure near this habitat (Robillard et al. 2010). In addition, the availability of

benthic substrates has been shown to influence habitat selection and distribution of juvenile flatfish (Stoner and Abookire 2002, Ryer et al. 2004). Unlike other modeling analyses of flatfish habitat use (Florin et al. 2009, Loots et al. 2010, Simpson and Walsh 2004, Zuchetta et al. 2010), models from the current study did not retain sediment variables. This may be due to the quality of data, given that sediment types were binomially represented without mention of a dominant sediment type or percent composition.

Southern flounder are a predominant predator of brown shrimp, a benthic crustacean, in Galveston Bay from March through September (Minello et al. 1989). Abundance of brown shrimp was only retained in the YOY-fall model in which intermediate abundances of brown shrimp increased occurrence of southern flounder. Although high densities of brown shrimp did not result in increased southern flounder occurrence, greater use of marsh edge and seagrass habitats by brown shrimp in the fall (Clark et al. 2004) may allow for some separation in the distribution of the two species within the GBC. Brown shrimp abundance was not retained in the newly settled or YOY-summer models, and this likely was due to the fact that southern flounder in these life stages are too small to consume brown shrimp (Kamermans et al. 1995).

In addition to benthic conditions, physicochemical parameters such as temperature can structure estuarine fish assemblage composition (Attrill and Power 2002), and higher temperatures in the GBC was associated with greater occurrence of southern flounder during the newly settled life stage. Although juvenile southern flounder can tolerate a wide range of temperatures, with a minimum tolerance of at least

4° C (Taylor et al. 2000), growth may be inhibited at temperatures less than 20° C (White and Stickney 1973), potentially explaining the negative effect of lower temperatures on the occurrence of newly settled southern flounder. Greater temperature variability also was associated with lower occurrence of newly settled southern flounder. Increased stability in temperature has been suggested to help facilitate recruitment of estuarine species (Drake et al. 2002). Temperature was not retained in either YOY models, and this may be due to greater physiological tolerance with ontogeny or elevated temperatures throughout the bay during the summer and fall.

Salinity is also regarded as an important environmental scalar, and it can directly or indirectly influence the distribution of suitable nursery habitat within an estuary (Secor and Rooker 2000). This chapter's results support this premise, and GAMs indicated that salinity played an important role in determining the distribution of YOY southern flounder in the GBC. Within the YOY-fall model, occurrence of YOY southern flounder in the GBC was increased at higher salinities, potentially to prepare the body for higher salinity of coastal waters that will be inhabited during the winter. This result, however, contrasts with the finding that southern flounder occurred near freshwater inlets and far from tidal inputs within the same YOY-fall model. Greater use of areas within 10 km of freshwater inlets also occurred during the preceding YOY-summer life stage. The conflicting results observed for the YOY-fall life stage between salinity and distance to water sources may represent the use of multiple habitat types during the first year of life. Starting in November and peaking in December, southern flounder aggregate at tidal passes and subsequently in coastal waters for reproduction (GSMFC

2000). It is therefore possible that southern flounder use areas near freshwater inlets for part of the YOY-fall life stage prior to moving into higher salinity waters to prepare for emigration out of the bay. Recent otolith microchemistry analyses also indicate that variation exists in the extent and timing of freshwater use by southern flounder within the first year of life (Lowe et al. 2011). Salinity was not retained in the newly settled model, and this may be because southern flounder are euryhaline as larvae (Deubler 1960). Increased variability in salinity, however, reduced the occurrence of southern flounder within both the newly settled and YOY-summer models, potentially indicating the physiological costs of increased environmental variability (Aranguren-Riano et al. 2011, Death and Winterbourn 1995).

Higher southern flounder occurrences observed in areas of turbidity higher than 30 NTU during the newly settled life stage suggests that these habitats may enhance growth or survival of southern flounder. Other studies have hypothesized that turbidity levels in Gulf of Mexico estuaries may provide protection from predators for juvenile fishes (Blaber and Blaber 1980), and other work has documented that predation is reduced in areas of moderate to high turbidity (Gregory and Levins 1998), with little impact on foraging success on small, slow-moving prey (De Robertis et al. 2003). High turbidity, however, may reduce foraging success for larger, YOY southern flounder feeding on more mobile prey, and subsequent tradeoffs between prey capture and predation risk may negate the benefits realized by newly settled southern flounder. These tradeoffs may explain why turbidity was not retained in either the YOY-summer or YOY-fall models.

Spatial arrangement of suitable habitat predicted for GBC varied among life stages, with older or larger southern flounder more common within large contiguous patches of suitable habitat. Presence of the newly settled life stage within more localized patches of suitable habitats may be related to the increased occurrence of southern flounder at seagrass beds. Complex habitats such as seagrass can reduce predation risk by providing a visual or physical impediment between predator and prey (Rooker et al. 1998), and seagrass beds can maintain high densities of juvenile fishes (Orth et al. 1984). Patches of predicted suitable habitats may become less localized with successive life stages because of a decreasing importance of using specific habitat types such as seagrass beds, greater physiological tolerance, or ontogenetic changes in behavior. Southern flounder mobility is expected to increase with ontogeny (body size), and the establishment of home range may occur during the first year of life, which can decrease patchiness of spatial distributions in fish in comparison to settlement stages if home ranges have little overlap among individuals (Methven et al. 2003). In addition, physiological tolerance may increase with ontogeny, as the number of physicochemical parameters retained in models decreased after the newly settled life stage. Decreased patchiness in the distribution of southern flounder also may help to explain the reduced model fit for the two YOY models in comparison the newly settled model, as the ability to generate strong species-habitat relationships is lower for species or life stages with greater spatial ranges and greater physiological tolerances (Planque et al. 2007, Sundblad et al. 2009).

The differences in habitat suitability among West Bay, Lower Bay, and Upper Bay can be attributed to their differences in benthic habitats, physicochemical conditions, and position relative to water sources within the GBC. West Bay contains the only known remaining seagrass beds in the GBC, because the beds in Upper and Lower bays were eradicated by the 1980s due to hurricanes, dredging, and urban development (Pulich and White 1991). The seagrass beds in West Bay are predicted to provide favorable habitat to newly settled southern flounder. Southern flounder were negatively associated with oyster reefs within the YOY-summer model. Oyster reefs are primarily located in West Bay and Lower Bay, and therefore these regions were predicted to have low suitability during the YOY-summer life stage. Lower Bay also is characterized by high environmental variability as indicated by spatial interpolations of TPWD data, which contributes to its low predicted suitability for newly settled and YOY-summer life stages. Upper Bay areas are a minimum of 20 km from tidal inlets, and this region has the greatest freshwater influence in the GBC, containing inlets for the Trinity and San Jacinto rivers (annual discharge rates during the study period of 13.1 m³/s and 217.8 m³/s, respectively; USGS 2012), and these areas represent suitable habitats for YOY-summer and YOY-fall life stages.

Here it is shown that a mix of temporal, benthic, and physicochemical characteristics influence habitat suitability of juvenile southern flounder within the GBC. Factors influencing habitat suitability were associated with season and ontogeny, indicating that suitable habitats used by juvenile southern flounder are dynamic. Suitable habitats of newly settled southern flounder that arrive to the GBC in the winter are near

seagrass beds with higher temperatures and greater environmental stability, whereas optimal habitats of older YOY fish in the summer and fall are away from tidal inlets and near sources of fresh water. The changes in habitat requirements for juvenile southern flounder indicate the importance of identifying life-stage specific essential habitats. Habitat distribution models that incorporate a variety of dynamic and static environmental characteristics will improve predictive capabilities and lead to more spatially resolved management of estuarine fishes and their habitats.

CHAPTER III

FINE-SCALE MOVEMENTS AND HABITAT USE OF JUVENILE SOUTHERN FLOUNDER (*PARALICHTHYS LETHOSTIGMA*) IN AN ESTUARINE SEASCAPE

Introduction

Habitat availability within a seascape can influence the movement of fishes by providing a mechanism for enhancing fitness through seeking optimal habitats (Kahler et al. 2001). Optimal or suitable habitats are those considered to improve an individual's fitness by increasing food availability and decreasing predation risk and/or metabolic costs. The suitability of potential habitat types or areas can vary with time, as factors influencing fitness (i.e. predation, food, and physicochemical conditions) are dynamic (Bowler and Benton 2004). Furthermore, the arrangement of habitats within a seascape can influence directedness and magnitudes of movement (McIntyre and Wiens 1999). Identifying habitats and/or areas that are used disproportionately is necessary for proper management of marine fishes, and information regarding the movements and linkages among habitat patches remains understudied (Boström et al. 2011).

Several methods have been used to investigate movement and habitat use of fishes. Traditional methods for determining movements include distributional studies, which compare abundance and size structure of fishes among areas or regions. These studies provide a snapshot of organism distribution within a seascape; however, information on movement or linkages across habitat types from such studies is limited. Conventional tagging studies can provide greater temporal resolution (depending upon

the number of recaptures), but are often characterized by low tag returns and still lack fine-scale resolution. The advent of electronic tags has allowed for more detailed understanding of fish movements and habitat selection (Cooke et al. 2004). Passive acoustic telemetry has the ability to describe broad-scale movements of estuarine or marine fishes (Heupel et al. 2004, Sackett et al. 2007, Wetherbee et al. 2007); however, information on specific habitat types used is limited with this approach. Although active acoustic telemetry allows for the construction of fine-scale movement patterns (Hitt et al. 2011, Papastamatiou et al. 2011), it is limited in duration, as animals are typically followed for a maximum of 24 hours. Recently developed technology bypasses the limitations of both techniques by using multiple, closely spaced passive receivers to triangulate fish positions, generating continuous records of fine-scale movements within a seascape (Espinoza et al. 2011a).

Southern flounder (*Paralichthys lethostigma*) are a recreationally and commercially important flatfish found in estuarine and coastal waters along the Gulf of Mexico and the southeast Atlantic Ocean. Recent analyses indicate a precipitous decline in the southern flounder population in the northern Gulf of Mexico (Froeshke et al. 2011) as well as reduced levels of recruitment (Náñez-James et al. 2009). While distributional studies (Glass et al. 2008, Náñez-James et al. 2009) and habitat distribution models (Chapter II) have determined species-habitat relationships for newly settled and young-of-the-year (YOY) southern flounder in the northern Gulf of Mexico, understanding of fine-scale movement over short time scales is lacking. The aim of the current study is to use acoustic telemetry to describe fine-scale movements of YOY

southern flounder and to relate these movements to available habitats within an estuarine seascape.

Methods

The current study was conducted in Christmas Bay, a small bay within the Galveston Bay complex (GBC) in Texas (Figure 5). Christmas Bay is a shallow estuary (mean depth ~0.7 m), and is unique among the subbays within the GBC because it contains the only significant stands of seagrass, both shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*) (Pulich and White 1991). In addition, a variety of other habitat types (sand, oyster reef, marsh edge) are in close proximity and often interdispersed in seagrass meadows, making Christmas Bay an ideal system for evaluating habitat connectivity. Bare substrates within the study area were generally comprised of sand-sized sediments with lower amounts of silt- and mud-sized sediments present at some locations. For simplicity all bare substrates will be collectively be referred to as sand.

Habitats within the study area were mapped using both satellite imagery and ground measurements. Orthorectified satellite images taken on 3 May 2010 (TNRIS 2010, available at <http://data.tnris.org/datadownload/quad.jsp?Quad=Christmas%20Point>) were used to delineate salt marsh, turtle grass, and oyster reef boundaries.

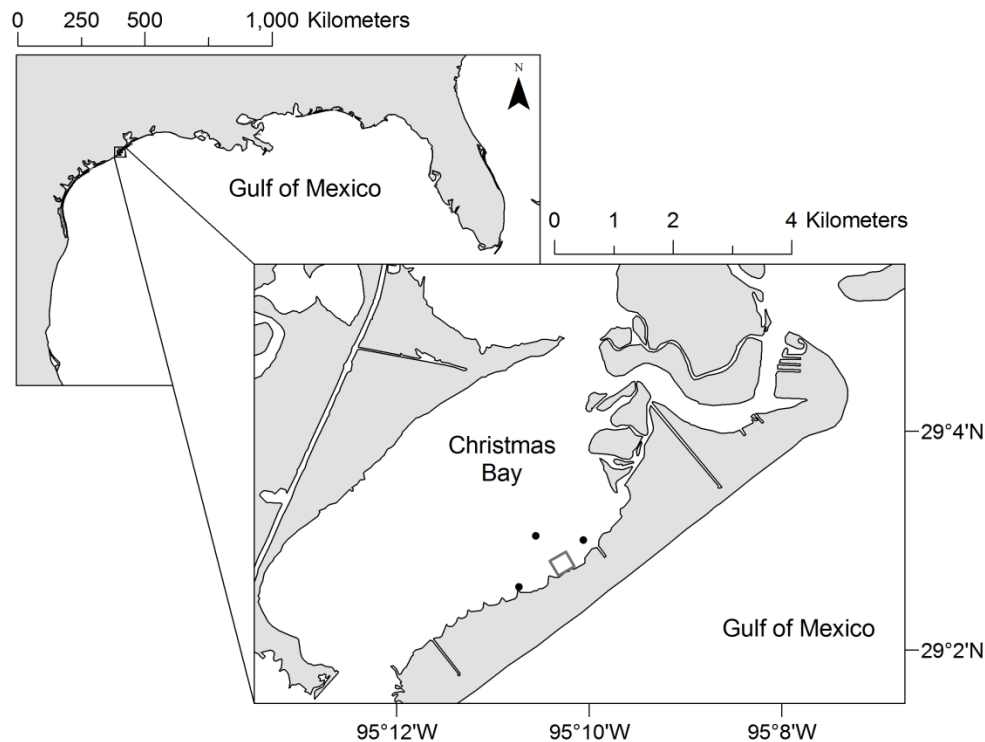


Figure 5: The location of the study area in Christmas Bay, Texas. The coverage area of the VPS array is denoted by the box within the inset, and the three surrounding points represent the positions of the three receivers external to the array.

In order to ground truth these habitat classifications, discriminate between shoal grass and sand, and record relative depth values across the study area, 235 random points within the study area were selected and examined in the field. At each point location, habitat type and depth (corrected for by tidal height) were recorded. Depths across the study area were then interpolated using universal kriging within ArcGIS's Spatial Analyst extension, and substrate slope (percent slope m^{-1}) was estimated at a 5 m^2 resolution (ESRI, Redlands CA). In addition to examining relative depth use, the realized depths occupied by southern flounder were estimated by correcting original recorded depths for tidal height. High and low tide predictions for Christmas Bay

(NOAA 2012) were used to fit nonlinear Loess smoothers within R 2.14 (R Core Development Team 2010). These smoothing functions were then used to predict the tidal height as a continuous variable for all times southern flounder were detected within the study area. Temperature and salinity in the study area were monitored during the study. Water temperature dataloggers (HOBO Inc, Cape Cod, MA) were affixed to each receiver and temperatures were recorded every 15 minutes to observe fine-scale and diel temperature cycles over the duration of the study. To examine temperatures experienced by tagged southern flounder, the recorded temperature from the datalogger on the receiver closest in distance to each fish location (at the closest possible time) was determined. Salinity at each receiver was measured weekly for four weeks during the trial.

Young-of-the-year (YOY) southern flounder (284-370 mm TL; Table 3) were captured via hook and line in Christmas Bay. Due to sexual dimorphism (i.e., males smaller than females), some individuals included in the study may have actually been age-1 or age-2 southern flounder (Stunz et al. 2000), but for consistency in terminology, all fish in this chapter will be referred to as YOY. Fish were held in a 1-m³ tank at the Texas A&M University at Galveston Wetlands Center for 4 to 7 days prior to tagging. During the tagging procedure, fish were anesthetized using clove oil, and V9 transmitters (Vemco Ltd, 9 mm x 24 mm, and transmits at random intervals between 60 and 180 s, corresponding to 80-100 days of battery life) were externally mounted on the eyed-side of each southern flounder following a protocol modified from Decelles and Cadrin (2009). Each V9 transmitter was placed in a latex sleeve and two nickel tagging

pins were passed from the blind side of the individual (held by a vinyl laminated tag (Floy Tag Inc, Seattle WA) through both the dorsal musculature and latex sleeve. The latex sleeve and pins were secured with rubber earring backings and a small metal crimping sleeve (Figure 6). Immediately prior to release, each southern flounder was examined for physical harm due to tagging.



Figure 6: YOY southern flounder with acoustic tag externally attached.

Table 3: Summary of recorded detections for tagged southern flounder. First Detection takes into account a 4-hour acclimation period. "# VPS locations used" indicates triangulated positions of fish that had an HPE equal or less than ten. The distance tracked within the VPS array ("D tracked in VPS") was calculated as the sum of the distances between each successive VPS location. The total estimated distance tracked for each southern flounder ("Total D tracked") includes both locations within the VPS array as well as the three "Outer stations." Outer stations were labeled as being approximately East (E), North (N), or West (W) of the VPS array.

Tag ID	TL (mm)	First Detection	Last VPS detection	Last Detection	# outer detections	Outer stations	# VPS locations used	D tracked in VPS (m)	Total D tracked (m)
T01	341	6/29/11 20:41	7/3/2011 7:17	7/7/2011	83	E, N, W	663	2,414	8,582
T02	350	6/30/11 4:05	7/1/2011 3:45	7/25/2011	58	N, W	94	528	4,168
T03	315	6/29/11 16:44	7/2/2011 3:37	7/5/2011	7	E, N	170	1,535	4,269
T04	284	6/29/11 22:38	7/6/2011 21:59	7/11/2011	9	E, N, W	185	1,303	4,402
T05	347	6/29/11 21:29	6/30/2011 6:27	6/30/2011	7	E, N	6	220	2,065
T06	370	6/29/11 22:17	7/7/2011 0:09	7/16/2011	1	N	99	1,605	2,271
T07	295	6/29/11 23:22	6/29/2011 23:48	6/30/2011	12	E, N	1	0	1,477
T08	358	6/30/11 3:36	6/30/2011 9:00	7/8/2011	6	E, N, W	60	413	3,588

Eight southern flounder were released in the study area and tracked using a Vemco VR2W Positioning System (VPS) in a section of Christmas Bay. The VPS in Christmas Bay was comprised of 10 closely-spaced (30-50 m apart) VR2W receivers, which allowed me to triangulate southern flounder positions to a potential accuracy of 2-6 meters (Espinoza et al. 2011b). Three additional receivers were placed outside the VPS approximately 600 to 800 m to the north, east, and west of the array to track larger scale movements (Figure 5). To ensure time synchronization of the internal clocks among VPS receivers, four sync tags (Vemco Ltd) were also placed within the VPS array. Tagged southern flounder were released on June 29, 2011, and the last detection by a single receiver occurred on July 28, 2011.

Prior to analyses, data were filtered by time and horizontal position error (HPE), which is a relative measure of horizontal error sensitivity. Only locations with an HPE < 10 were included in analyses. Generally, HPE < 10 corresponded to positional errors of < 5 m (mean = 1.4 m, SE = 0.02 m) when examining errors of static tags placed within the array, similar to other VPS studies (Espinoza et al. 2011b). In addition, detections within the first 4 hours of the study were removed from analysis to account for the acclimation period of fish to the study site.

Data Analyses

Movements of tagged southern flounder were characterized by estimating step lengths between successive VPS locations using Hawth's Analysis Tools extension in ArcGIS (Beyer 2004). Step lengths and the time elapsed between successive points were

then used to calculate step speed. As missed detections could result in the underestimation of step speeds, mean step speed was calculated using only detections without missed transmissions (occurring successively within 3 min). Differences in mean step speeds among habitat types were examined with a paired t-test. Step lengths were summed to estimate the distance tracked within the VPS array, and VPS locations were combined with detections made by the three receivers located outside of the array to estimate total tracked distance. Because there is no way to determine the directionality or distance of a fish detected by an individual receiver, the location of any southern flounder detection made by an outer receiver was assumed to be that of the receiver itself.

Habitat use was analyzed with a Euclidean distance-based approach, which uses individual fish as the sampling unit and thus does not require error modeling (Conner et al. 2003). Even if habitat classification error occurs, the distance to the correct habitat is reduced using this approach (Conner and Plowman 2001). Nonrandom habitat use was tested according to Conner and Plowman (2001). Within the VPS array's coverage, 1000 random points were generated inside an area within 80 m of any three or more VPS receivers, representing the range at which I am confident that the system could detect a tagged southern flounder. Distances between each random point and each habitat (salt marsh, oyster reef, sand, shoal grass, turtle grass) were determined and then averaged to generate a vector of mean distances to each habitat type. For each VPS location (i), the distance to all habitat types was also determined (note: distance to the habitat occupied by the fish at the time of detection was 0) (Conner et al. 2003, Conner and Plowman

2001, Miller et al. 2000). Each EDA ratio for southern flounder was based on the mean distance to each habitat type divided by the mean distance between random points and the same respective habitat type. If habitat use is random, all EDA ratios should equal one. Multivariate analysis of variance (MANOVA) was used to determine if EDA ratios differed significantly from a vector equal in length to the number of habitat types investigated (five) for which each value is one. If MANOVA results indicated a significant difference, univariate t-tests were then used to determine which habitat types were used disproportionately by comparing each habitat's EDA ratio to one. Pairwise comparisons were also used to test for differences in the utilization of each habitat between diel periods (day or night) and between rising and falling tides. Daytime was defined as the period of time between sunrise and sunset, and nighttime hours were considered between sunset and sunrise. Type of tide was defined using the National Oceanic and Atmospheric Association Tide Predictions Program data (NOAA 2012, available online: co-ops.nos.noaa.gov/tide_predictions.shtml). For all parametric statistics, $\alpha = 0.05$.

The relative importance of species-habitat relationships for tagged southern flounder were further quantified and weighed with a habitat modeling analysis similar to that of Aarts et al. (2008). VPS locations from all southern flounder were pooled along with an equal number of random points ($n=1284$) generated to represent locations where southern flounder were absent. Each random point was selected from the same area used for EDA analysis, within 80 m of three or more VPS receivers. In addition, each generated point was located within 67 m of a single VPS location. This distance

represents the average maximum distance observed between potential detections (based on the average observed maximum speed of 22.5 m/min and the maximum delay of 3 min between tag transmissions). These constraints are used to prevent absences from representing locations that either could not be realistically reached by southern flounder (given the previous location), or could not be reliably detected by the VPS, even if a fish was present. In addition, each randomly generated point was treated as occurring at the same time as a single VPS location so that the effects of temporally dependent variables (temperature and tidal height) could be investigated. By having a pair of points at each time, however, strictly temporal variables such as diel period could not be included in the analysis. All VPA locations and randomly generated locations were linked to four covariates: habitat type, relative depth, temperature, and slope (percent per meter). In addition, the interaction between relative depth and tidal height was investigated.

To investigate species-habitat relationships, generalized additive models (GAMs) were employed. Penalized cubic regression splines determined the shape of nonparametric functions, with the degree of smoothing selected automatically for models and generated within the “mgcv” library (Wood 2006, Wood 2008) using R 2.14 software (R Development Core Team 2010). To prevent overfitting, limits can be placed on the degrees of freedom (df) given to each response curve (Cianelli et al. 2008), and in this study the response curve for each variable was limited to a maximum of four df. All possible model combinations were generated and compared using percent deviance explained and the Akaike Information Criterion (AIC) (Akaike 1974). A final model was selected by minimizing the AIC score. Additional models, each with a single covariate

removed from the final model, were generated to calculate the change in percent deviance explained in an attempt to understand the relative importance of covariates retained in the final model.

Results

A total of 2,210 locations were calculated using the VPS array, of which 1,284 had an associated HPE of less than 10 and occurred at least four hours after the trial start. Because few VPS locations were detected for two fish, these data were omitted from habitat use and movement analyses using the individual southern flounder as the sampling unit (EDA ratios, L_i values, and step speeds).

Movements

All eight southern flounder were detected by both the VPS array and by at least one of the three additional receivers placed to the east, north, and west of the VPS array. Three southern flounder were detected by all three of the outer receivers. The number of times individual southern flounder were detected by the outer receivers ranged between 1 and 83 (Table 3). When southern flounder left the VPS array they were generally

detected by the receiver east or north of the VPS array. Although four of the southern flounder were detected by the receiver west of the array, these fish were always observed by the north or east receiver first. The total tracked distances of southern flounder within the VPS array ranged between 412 m and 2414 m (Figure 7). When accounting for larger scale movements detected by the three outer receivers, the total distances tracked among southern flounder ranged between 1477 m and 8582 m (mean = 3853 m \pm 2215 SD). If only concurrent detections (those within 180 seconds of each other) were used, average speed of southern flounder with the VPS array was 4.2 m/min (\pm 1.1 m/min SE) and a relative speed of 12.3 body lengths/min (\pm 2.9 body lengths/min SE). Average maximum speed observed among southern flounder was 22.5 m/min (\pm 6.4 m/min SE), and the maximum speed among southern flounder ranged between 6.4 m/min and 52.4 m/min. Step speed was not influenced by southern flounder body size (linear regression, $p = 0.59$), diel cycle (t-test, $p = 0.80$) or habitat (ANOVA, $p = 0.47$).

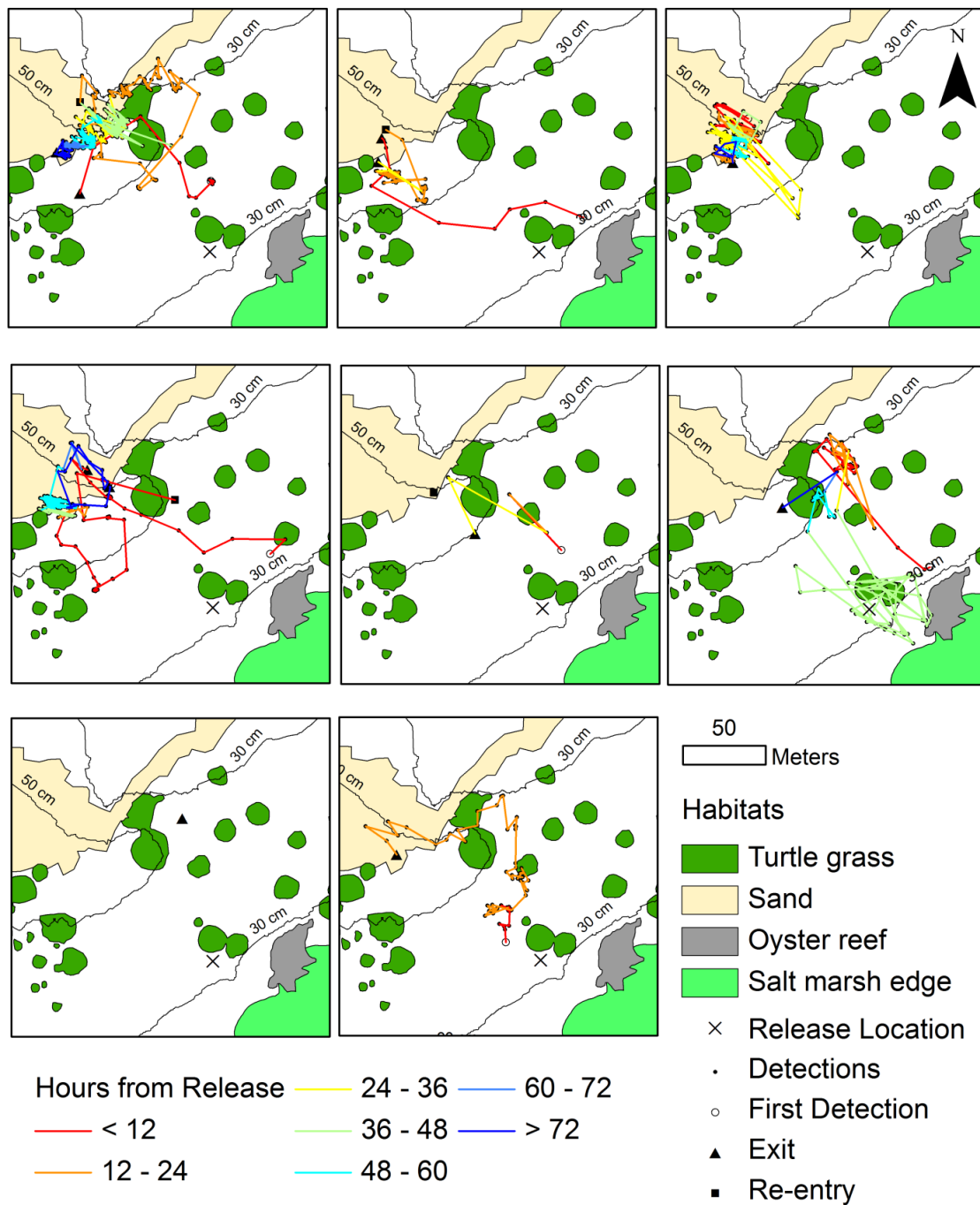


Figure 7: Detections of YOY southern flounder within the VPS array. Exits are defined as detections for which the next detection occurred on one of the three receivers exterior to the VPS array. Re-entry detections were considered those to occur within the VPS when the previous detection occurred on one of the exterior receivers.

Habitat Use

Areal coverage of habitats within the VPS array were shoal grass (74.2%), turtle grass (10%), sand (8.8%), salt marsh edge (within 10 m of the salt marsh, 4.6%), and oyster reef (2.4%) (Table 4). Greater than 95% of all VPS locations observed for southern flounder were located in either sand (53.9%) or shoal grass (42.1%) habitats. The proportion of VPS locations of southern flounder in the other habitats was markedly lower: turtle grass (3.8%), oyster reef (0.2%), and salt marsh (0.0%). Because of the limited number of detections in salt marsh and oyster reef, these habitat types were excluded from GAM and step speed analyses. Habitat use analysis based on EDA ratio indicates nonrandom selection of habitat types. Southern flounder locations were significantly closer to sand than random points (mean EDA = 0.36, MANOVA, $p = 0.01$) and significantly farther from salt marsh than random points (mean EDA = 1.46, MANOVA, $p = 0.02$) (Figure 8). The use of other habitats, including turtle grass ($p = 0.21$), oyster reef ($p = 0.07$), and shoal grass ($p = 0.23$) were found to be random using EDA ratios. These trends persist throughout the diel cycle, as paired t-tests indicated no change in EDA ratios either between day and night in all five habitats ($p > 0.05$), or between rising and falling tides ($p > 0.05$).

All potential GAMs were investigated, and deviance explained by the final model was 17.8% (AIC 2945). The final model included the covariates habitat, relative depth, slope, temperature, and the interaction between relative depth and tidal height. Response plots indicated that southern flounder occurrence was highest for sand habitats followed by shoal grass and then turtle grass (Fig. 9). Zero locations were detected on

oyster reef, resulting in a negative coefficient for this habitat type, and a wide confidence interval. Removal of habitat type from the final GAM resulted in a 1.8% decrease in deviance explained.

Table 4: Summary of habitat composition within the VPS array.

Habitat	Available habitat (m ²)	% available habitat	Total locations within	% locations
Shoal grass	22,590	74.2%	540	42.1
Turtle grass	3,051	10.0%	49	3.8
Sand	2,683	8.8%	692	53.9
Salt Marsh	1,403	4.6%	0	0.0
Oyster Reef	723	2.4%	2	0.2

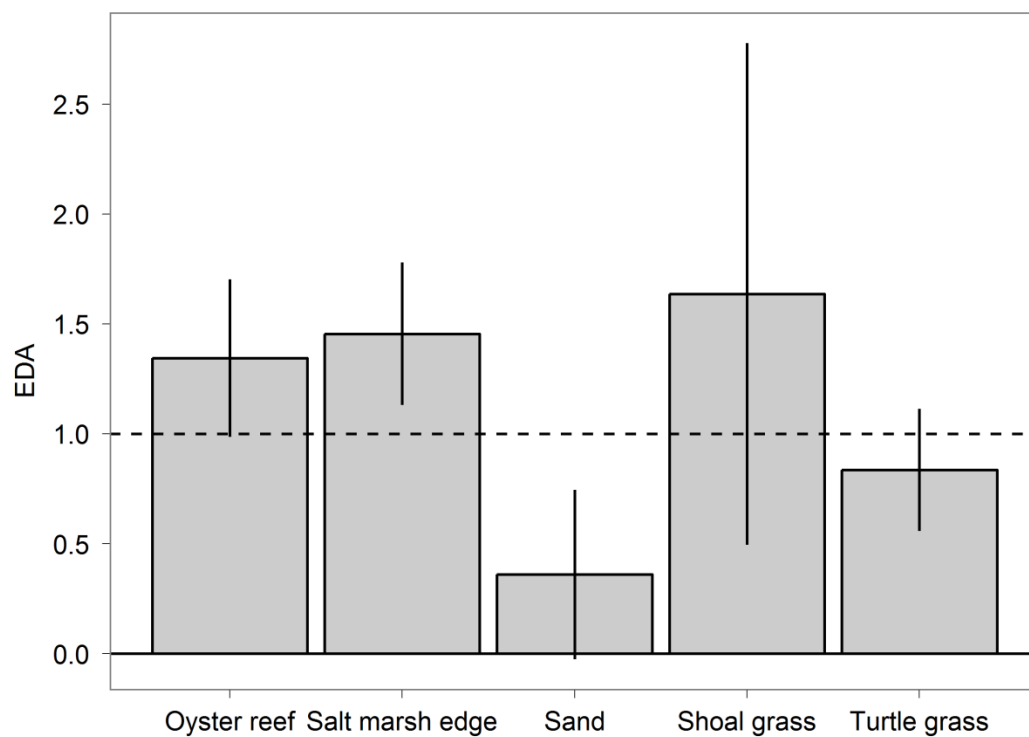


Figure 8: Mean EDA ratios of habitat types available to southern flounder within the study area. Values less than one indicate greater than random use, while values less than 1 indicate avoidance.

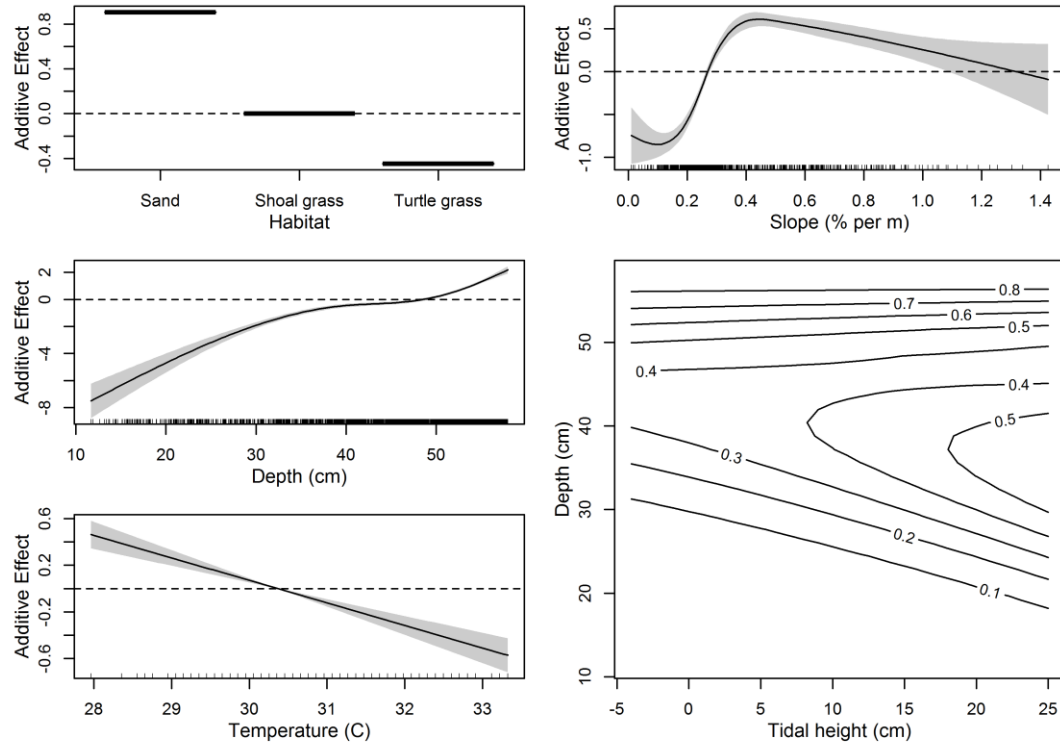


Figure 9: Response plots of explanatory covariates on the occurrence of southern flounder tracked with acoustic telemetry as analyzed with GAM. The isopleths on the contour plot indicate the additive effects of the interaction between water depth and tidal height on southern flounder position.

Bathymetric and physicochemical variables also significantly influenced southern flounder occurrence. Relative depth was found to be the most influential covariate within the final GAM, and the response curve indicates increased use of depths greater than 50 cm by southern flounder and decreased use of depths less than 50 cm (Fig. 9). Deviance explained decreased by 5.4% when depth was removed from the final GAM. Relative depth use was influenced by tide, with southern flounder using shallower parts of the study area at higher tidal heights. The removal of the interaction

between relative depth and tidal height from the final GAM reduced the deviance explained slightly (1.1%). Slopes were generally shallow within the VPS array, varying between 0.0% and 1.4% m^{-1} , and the occurrence of southern flounder was greatest in areas with slopes between 0.3% and 1.0% m^{-1} (Fig. 9). When slope was removed from the final model, deviance explained declined by 2.0%. The temperatures experienced by southern flounder within the VPS array ranged between 28.7 °C and 32.8 °C, with a mean of 30.2 °C (± 0.73 °C SD). GAM analysis indicated a negative relationship between water temperature and southern flounder occurrence, and the response plot showed that occurrence increased at temperatures less than 30.5 °C (Figure 9). At any given time the difference between minimum and maximum temperatures was generally < 1.0 °C and never greater than 2.0 °C. Temperature was considered the least important variable in the final GAM, because the removal of this variable decreased percent deviance explained by 0.4%

Discussion

The current study described fine-scale habitat use and movements of juvenile southern flounder within a shallow estuarine seascape. Detections on receivers outside the VPS array indicated that YOY southern flounder can move up to 2 km per day, and 8.5 km over ten days. Due to the small spatial extent of the study, these estimates should be considered conservative, as actual movements are probably greater. Mean overall and maximum step speeds based on VPS data (4.2 m/min and 22.5 m/min, respectively) also demonstrate a potential for a high degree of movement on small spatial scales. These

findings suggest that YOY southern flounder remained active the majority of the time they were being tracked, but at the same time stayed within a relatively small area. Similar dispersal behaviors have been reported for other estuarine-dependent paralicthyids such as summer flounder (*Paralichthys dentatus*) (Sackett et al. 2008).

Benthic seascape structure and habitat types can influence the movements of fishes (Farrugia et al. 2011, Hitt et al. 2011, Semmens et al. 2009). Selection of habitats can change during ontogeny for flatfish, with structurally complex habitats (i.e., seagrass) often used immediately after settlement followed by a transition to habitats without vegetation at larger sizes (Busby et al. 2005, Sackett et al. 2008, Stoner et al. 2001). Similarly, distributional studies indicate that newly settled southern flounder often reside in areas near or within seagrass beds (Glass et al. 2008, Nanez-James et al. 2009) and then move away from these complex habitats near the end of the YOY stage (Chapter II). EDA ratio and GAM analyses of acoustic tracking data appear to support the previously reported ontogenetic shift, with YOY southern flounder preferring habitats with limited complexity (i.e., sand habitat) relative to seagrass or other structurally complex habitats assumed to be important for younger, newly settled individuals. The higher occurrence of southern flounder in bare substrate within Christmas Bay may be due to the fact that the sand substrate provides an appropriate environment for utilizing cryptic behaviors common with flatfish, such as burying or matching substrate color, which is known to decrease predation rates (Fairchild and Howell 2004, Ryer et al. 2008) and increase foraging efficiency (Gronkjaer et al. 2007, Nordstrom and Booth 2007) of flatfishes.

Aside from habitat, bathymetric features, including depth and slope, can influence distributions of marine fishes. Fishes within estuaries often demonstrate depth preferences (Gibson et al. 2011), and depth has been shown to influence an individual's predation risk (Ryer et al. 2010). Water depth was identified as the most influential variable in GAM analysis, with YOY southern flounder using deeper waters (> 50 cm relative depth) within the VPS array. In addition, most detections occurring outside of the shallow VPS array occurred on the receiver north of the array, which had the greatest depth (~ 100 -cm depth). Depths across the VPS array were relatively shallow (< 70 cm at low tide) and the avoidance of shallow water habitats within the VPS array (< 50 cm) may minimize vulnerability to avian predators (Bancroft et al. 2002). When southern flounder exited the VPS array, they were generally detected on the receiver 600 m to the north, an area of Christmas Bay deeper than both the VPS array and the areas surrounding other receivers to the east and west of the VPS array. In addition to depth, slope of the substrate can constrain use by fishes within riverine (Santoul et al. 2005) and coastal systems (Letourneur et al. 2003). YOY southern flounder appear to prefer shallow slopes, which may allow for more efficient and complete burying than steeper areas. Southern flounder occurrence was increased in the western portion of the array adjacent to the sand bar, where slopes were shallow.

Increased environmental variability may limit the distribution of fishes in fluvial and estuarine habitats (Beesley and Prince 2010, Love et al. 2009). Variability in temperature in Christmas Bay may be mediated by water depth, with deeper areas experiencing smaller ranges on a diel basis. Temperature dataloggers placed in deeper

locations exhibited diel variations in water temperature less than 2.5 °C, while those in the shallowest parts of the array ranged from 4.0 – 6.0 °C. Reduced exposure to variations in physicochemical conditions such as temperature may reduce metabolic and physiologic costs (Keiffer and Wakefield 2009). Tides also introduce environmental variability, altering depths of estuarine systems on a cyclical scale and potentially impacting fish movements (Sakabe and Lyle 2010). It was observed that high tides increased southern flounder use of shallower parts of the study area, indicating that suitable habitat was dynamic and varied temporally.

Physicochemical factors can act as scalars that shape the distributions of fishes at multiple spatial scales (Attrill and Power 2002, Secor and Rooker 2000, Selleslagh and Amara 2008). Physicochemical conditions also influence metabolism, and decreased temperatures may mediate potentially negative impacts of low dissolved oxygen on growth rates of southern flounder (Del Toro-Silva et al. 2008). In fact, temperatures of 27 °C and 29 °C maximized growth rates of southern flounder in controlled experiments, while temperatures above 30 °C resulted in zero or negative growth rates (Del Toro-Silva et al. 2008). The temperatures selected by southern flounder tracked with acoustic telemetry were similar, with areas with temperatures > 30 °C being avoided. Although temperature is increasingly implicated as an important influence on distribution, condition, and growth of flounder (Del Toro-Silva et al. 2008, Methratta and Link 2007, Vasconcelos et al. 2009), it was the least important covariate in GAM analysis. However, the ability to detect temperature's importance may be reduced due to the small spatial extent of the VPS array and corresponding low variability in water temperatures

across the study area. The study occurred during a period of severe drought throughout Texas, and salinity was relatively high for Christmas Bay at the trial start (36) and continued to rise throughout the study. During the week of the last fish detection (July 28, 2011), salinity reached 40 at several locations. Despite the fact that I was unable to relate salinities to southern flounder movements, it is expected that this parameter influences habitat use, as salinity gradients often impact flatfish distributions, including southern flounder (Allen and Baltz 1997, Walsh et al. 1999). Reduced model fit observed with GAM analysis indicates that additional physicochemical factors may affect the movements of southern flounder.

We describe the fine-scale movements of YOY southern flounder within an estuarine seascape in the context of habitat, bathymetric, and physicochemical influences. Of these effects, depth, slope, and habitat type were most important in determining seascape use, with deeper sandy areas with shallow slopes being used most. To a lesser extent, temperature and tidal height also impacted use. In addition, results suggest that depth use may be modified by tidal cycles, demonstrating the potential dynamics of habitat use. Telemetry studies that successfully identify movements and habitat use at multiple spatial and temporal scales simultaneously will improve understanding of the habitats required to complete the juvenile stage, which is necessary information for efficient management (Beck et al. 2001).

CHAPTER IV

SUMMARY AND CONCLUSIONS

The study provides important information on the factors influencing southern flounder habitat use and movement. Using GAMs, it was determined that habitat requirements for southern flounder change with ontogeny and/or season, even within the first year of life. Newly settled southern flounder were most influenced by temperature and its corresponding variability in addition to the presence of seagrass beds. YOY southern flounder begin to show increased use of freshwater inlets during summer months, a trend that continues into the fall months. In addition, southern flounder decreased their use of tidal inlets during the fall. Intermediate abundances of brown shrimp, a potential prey item, also increased use by YOY southern flounder during this time. Predictions of the spatial arrangement of suitable habitats across the Galveston Bay complex indicate that the factors influencing southern flounder occurrence change with season and ontogeny, with more suitable habitats predicted within West Bay during the newly settled life stage, within Upper Bay during the YOY-fall life stage, and within West Bay and Upper Bay during the YOY-summer life stage. These results indicate the importance of long-term sampling surveys as well as the applicability of GAMs as a valuable type of habitat distribution model for determining species-habitat relationships. The results also demonstrate dynamic changes in habitat use during the first year of life for southern flounder.

With acoustic telemetry, it was apparent that habitat use by southern flounder was nonrandom and influenced by benthic and physicochemical conditions. EDA and GAM analyses of telemetry data indicate that southern flounder used sand habitats rather than seagrass, oyster reefs, or salt marsh edges. Analysis of telemetry positions with a GAM also indicated that depth and water temperature were important determinants of habitat suitability for YOY southern flounder, with individuals preferring deeper and cooler regions of the water column in Christmas Bay. In addition, southern flounder depth use was impacted by tidal height, suggesting that movements were influenced by tidal cycles at a fine spatial scale. Southern flounder occurrence was also increased at water temperatures less than 30.5 °C and therefore spatial-temporal changes in physicochemical conditions can impact southern flounder habitat use and movement. Southern flounder also demonstrated an ability to exploit larger spatial scales (~10 kilometers) over relatively short (weekly) temporal scales.

Both GAM and acoustic telemetry analyses indicate that habitat use by juvenile southern flounder, an estuarine-dependent species, is dynamic across multiple spatial and temporal scales. Combined these results suggest that distributions and movements of southern flounder are influenced by ontogenetic changes in habitat associations, temporal and spatial variability in physicochemical conditions, and tidal cycles. Therefore, it is necessary to consider discrete life stages and temporal intervals when defining essential habitats for this species during estuarine residency.

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VITA

Name: Nathaniel B. Furey

Address: 200 Seawolf Parkway
Ocean and Coastal Studies – OCSB Bldg 3029
Texas A&M University at Galveston
Galveston, TX 77553

Email Address: n.b.furey@gmail.com

Education: B.S., Marine Biology and Environmental Science, The University of
New England, 2009